

# Integration of Demographic Analyses and Decision Modeling in Support of Management of Invasive Monk Parakeets, an Urban and Agricultural Pest

Michael J. Conroy and Juan Carlos Senar

**Abstract** We investigated from 2003 to 2006 the population dynamics of Monk Parakeets (*Myiopsitta monachus*), an invasive, exotic, pest species inhabiting north-eastern Spain. Our study focused on several colonies of parakeets in Barcelona. Starting in 2003, we trapped and marked birds at the main Barcelona colony in Ciutadella Park during 2 annual periods: winter (pre-nesting) and late summer (post-nesting), respectively. We marked 459 individuals, and subsequently reencountered marked birds at the colony via recapture, and additionally obtained resightings of parakeets throughout Barcelona ( $n = 381$  recaptures and 570 resightings). We used a variation of the Robust Design in conjunction with reverse-time CR modelling to estimate survival and recruitment rates, and to determine the relative contribution of survival and recruitment to population growth rate. Due to high dispersal, apparent survival rates were low, so we used the combined recapture-resighting data to provide more realistic estimates of demographic survival. We then combined the projections with estimates of survival and recruitment elasticity from our statistical models in a decision model, in order to investigate alternative management scenarios for reducing damage from continued parakeet expansion. Given the logistical and social constraints under which managers operate, it appears that the most effective management strategy would be removal by trapping (in urban areas) or shooting (in rural areas) of birds during summer-winter period.

## 1 Introduction

Exotic species are now recognized as one of the leading global threats to native biodiversity and ecosystem function (Temple 1992; Kolar and Lodge 2001; Stockwell et al. 2003). They also cause significant economic losses (Pimentel et al. 2000), but their control and removal is normally difficult, and to succeed, requires previous appraisal and study (Feare 1991; Myers et al. 2006).

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M.J. Conroy (✉)

USGS, Georgia Cooperative Fish and Wildlife Research Unit, University of Georgia, Athens, GA 30602, USA

e-mail: mconroy@uga.edu

The Monk Parakeet (*Myiopsitta monachus*) is a typical invasive, exotic, pest bird species. The increase in parrot trade in recent years has facilitated its spread from South America into North America and Western Europe (Hyman and Pruett-Jones 1995; Van Bael and Pruett-Jones 1996; Cassey et al. 2004). The species is considered as a pest in most parts of its range, causing agricultural damage, injuring ornamental trees by picking up small branches for nest-building, damaging electric lines and other human made structures during nesting, acoustic contamination, and problems with falling nests (Bucher and Bedano 1976; Bucher and Martin 1983; Bucher 1984; Temple 1992; Bucher 1992).

The species has been especially successful in Barcelona, Spain, with the city containing one of the largest populations in western Europe (Domènech 1997; Domènech et al. 2003). Monk parakeets became established in Barcelona city in the early seventies, and by 2001 had reached 1441 ( $\pm 265$ ) individuals, with 313 nests, growing at an average 8% annual rate over 1994–2001 (Domènech et al. 2003).

Economic losses associated with the increase in parakeets have been partially quantified by Senar and Domènech (2001), who conducted surveys of damage in the agricultural area of Baix Llobregat, specifically in the municipalities of Prat de Llobregat, Sant Boi de Llobregat, Viladecans and Gavà. Senar and Domènech (2001) focused on damage to tomatoes, which is the main crop in the area, and prone to damage by parakeets. The birds also damage fruit trees and maize, but these fields are of much lower economic importance in the area. Senar and Domènech (2001) estimated that parakeets damaged 93,679 tomatoes (71,000–136,000). Assuming an average price of 0.50 €/kg and that 1 kg represents about 6 tomatoes (5–9), this translates to an estimated loss of 7,800 € (6,000–11,400 €) during 2001.

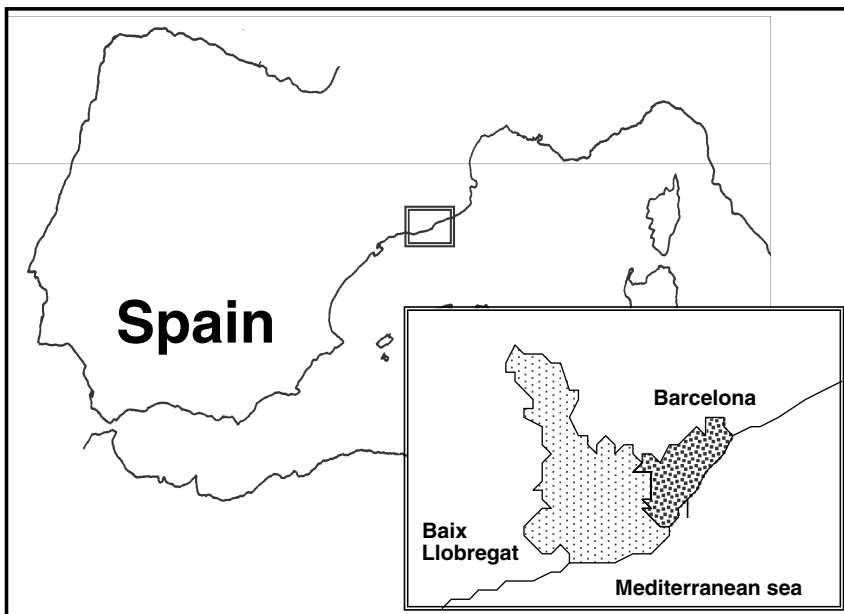
Damage by parakeets also occurs within Barcelona city but is more difficult to quantify. Birds harvest large number of branches during nest construction, and damage to trees (especially *Platanus* sp.) can be locally significant (Senar and Domènech 2001). Nests are built high (8–15 m) in trees and present a risk of human injury and property damage when they are dislodged during storms (Senar and Domènech 2001). Finally, large colonies of birds are very noisy and create disturbance around human dwellings; to mitigate complaints and minimize damage from falling nests, nests are periodically removed by the City Council. The costs of damage due to birds and nests, and of efforts to reduce these damages, are, however, poorly quantified.

The aim of this paper is to construct a decision support model that incorporates existing demographic data on Monk Parakeets, in order to evaluate alternative means of controlling the increase of parakeet populations.

## 2 Methods

### 2.1 Study Area

Monk Parakeets were studied in Barcelona city and the Baix Llobregat area, north-eastern Spain. The Baix Llobregat area is a traditional agricultural area in the



**Fig. 1** Location of study areas for Monk Parakeets in Spain, 2003–2006

Llobregat river delta, located 10 km south of Barcelona (Fig. 1). The land is mostly flat and with intensive irrigated agriculture, comprised of many different vegetables. Damage by parakeets, is however concentrated on tomatoes, maize and fruit trees.

## ***2.2 Capture–Recapture and Resighting***

We used a variation on the Robust Design (Williams et al. 2002) to allow for estimation of key demographic parameters over 26-month periods, the first (winter–summer; Table 1) of which includes the principal breeding period of parakeets. We obtained capture–recapture data over 6 primary (assumed to be open to survival, recruitment, and movement) and 23 secondary occasions (assumed closed to these factors) from November 2003 to August 2006. We captured and recaptured parakeets with a Yunick Platform Trap ( $2 \times 1 \times 1$  m; Yunick 1971) located at the Natural History Museum of Barcelona, within the Ciutadella Park in Barcelona city, which holds the larger Monk Parakeet colony within the Barcelona city (Domènech et al. 2003) (Fig. 2). Birds were marked with numbered aluminium rings and with special numbered medals, which could be read without having to trap the bird (Ingram 1977). We marked a total of 459 individuals, obtaining 381 recaptures between November 2003 and October 2006. We also obtained 570 resightings of individually marked birds during November 2003–March 2006. During the study period, we obtained resightings via reports from birdwatchers throughout Barcelona, and

**Table 1** Encounter periods and survival/emigration intervals for capture-recapture, resighting, and recovery analysis of Monk Parakeets in Barcelona, Spain, 2003–2006

Month	Year	Primary period	Secondary period	Interval length (d) <sup>a</sup>
Nov–Jan <sup>b</sup>	2003–2004	1	1	16
			2	16
			3	15
			4	222 <sup>c</sup>
Aug–Sep <sup>d</sup>	2004	2	1	16
			2	15
			3	105 <sup>e</sup>
			4	179 <sup>c</sup>
Dec–Feb <sup>b</sup>	2004–2005	3	1	16
			2	15
			3	179 <sup>c</sup>
			4	15
Jul–Sep <sup>c</sup>	2005	4	1	16
			2	15
			3	15
			4	15
			5	124 <sup>e</sup>
Jan–Mar <sup>b</sup>	2006	5	1	16
			2	15
			3	15
			4	156 <sup>c</sup>
Aug–Oct <sup>c</sup>	2006	6	1	15
			2	15
			3	26
			4	

<sup>a</sup> Interval between end of sampling period and beginning of next primary or secondary period.

<sup>b</sup> Winter capture period.

<sup>c</sup> Winter–summer interval.

<sup>d</sup> Late summer trapping period.

<sup>e</sup> Summer–winter interval.

observations made during the course of other activities, such as censusing parakeet nests. These observations were augmented by a citywide survey over 235 h in the summer of 2004 via a series of transects throughout Barcelona (Senar and Carrillo-Ortiz 2005); this latter effort resulting in 216 of the 570 total resightings. The resightings were then grouped, along with captures and recaptures, according to primary (open) and secondary (closed) occasions for subsequent analysis (Table 1).

## 2.3 Statistical Analyses

### 2.3.1 Components of Population Growth

We initially used the Robust Design and Pradel's temporal symmetry model (Williams et al. 2002) with the Huggins full heterogeneity models to estimate apparent survival ( $\phi$ ) and recruitment ( $f$ ) between each of the primary periods, as implemented in program MARK (White and Burnham 1999). This model provides estimates of abundance ( $N$ ) at each primary period as derived parameters. Estimates of population growth rate ( $\lambda$ ) and seniority ( $\gamma$ ) can be computed either by reparameterizing the Pradel model, or as derived parameters via

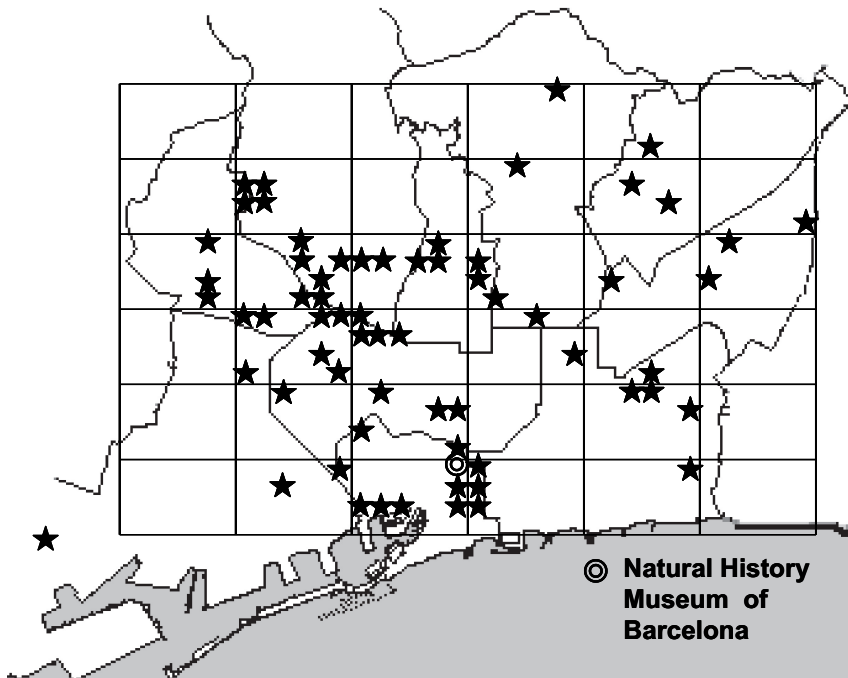


Fig. 2 Locations of Monk Parakeet colonies in Barcelona, Spain, 2003–2006

$$\hat{\lambda}_t = \hat{f}_t + \hat{\phi}_t \tag{1}$$

and

$$\hat{\gamma}_{t+1} = \frac{\hat{\phi}_t}{\hat{\phi}_t + \hat{f}_t}, \tag{2}$$

with estimated variances computed via the delta method (Williams et al. 2002: Appendix F). Expression (2) estimates the proportional contribution of survival to population growth at  $t+1$ , important for our later consideration of strategies to optimally control parakeet populations. We preferred the  $\phi, f$  parameterization over the  $\phi, \lambda$  or  $\phi, \gamma$  parameterizations available in MARK (White and Burnham 1999) because constraints such as  $\phi_t = \phi$  or  $f_t = f$  can be specified independently, whereas constraints such as  $\lambda_t = \lambda$  force a dependency with the remaining parameter (in this case  $\phi$ ). We evaluated goodness of fit under the Pradel model first via program RELEASE (from the MARK interface), which provides a general test of fit for CJS-type models. We also conducted 500 bootstrap simulations under the most general (time-specific survival and recapture) CJS model corresponding to these data, and compared the average deviance value from these simulations to the deviance obtained under this model for our data, finally taking the ratio of the latter

to the former as an estimate of  $c$ . We then applied this factor to our estimates and AIC values under the Pradel model, to adjust for overdispersion.

We note that our data and the Pradel model do not allow for complete identification of parameters of biological interest. First, the parameter  $\phi$  is denoted apparent survival, because it is the product of the probability of demographic survival ( $S$ ) and fidelity ( $F$ ); thus, to the extent that emigration from the study area occurs,  $\phi$  will underestimate  $S$ . Second, our estimates of the parameter  $f$  cannot separate between in-situ recruitment, and immigration from other sites. We used the joint recapture-resighting data and the Barker (1997) model to address the former problem and to obtain estimates of  $S$  and  $F$ . We used the data from the Robust Design (Table 1) to estimate survival, fidelity, return, recapture and resighting, with survival and fidelity rates constrained to one and return rates constrained to zero over the secondary (closed) periods. Because no dead recoveries occurred during the study period, we constrained recovery parameters ( $r_t$ ) to be zero. As with the Pradel analyses, we evaluated goodness-of-fit via bootstrap simulation, adjusting subsequent model comparisons and confidence intervals by the variance inflation estimate as necessary. Our study design, and inability to accurately determine ages of captured birds, precluded us from addressing the latter problem, with implications for the application of our estimates to the decision problem, considered further below.

### 2.3.2 Decision Model

A decision model requires 3 components: (1) a quantitative statement of the objective, (2) delineation of decision alternatives, and (3) a model relating the decision alternatives or controls to the objective. The task then is to determine the combination of decisions that best meet the resource objective, taking into account biological, economic, or other constraints.

In our case, the biological objective is to reduce population numbers or growth of parakeets, so as to reduce economic and other damages. For either urban or rural situations, economic loss occurs, and it is thus desirable to reduce the number of parakeets. Because we cannot necessarily quantify these losses (particularly for urban birds), we will henceforth assume that the goal is to reduce the losses by reducing number of birds, and use our population and catch-effort models to provide guidance as to the most efficient ways to do so.

The decisions at our disposal include removal of adult and flighted juvenile birds via trapping or shooting, and removal of nests. These controls are assumed to relate to specific parameters of survival ( $S$ ) and recruitment ( $f$ ). The exact form of our decision model depends on a number of considerations, including the availability of appropriate information for costs and other constraints. First, we specified controls and model outcomes in terms of per-capita rates, because our most reliable data was in these terms. Second, we considered objective functions of 2 forms: (1) meeting a biological objective (reduced growth), subject to economic and other constraints; and (2) meeting a cost objective, subject to biological constraints. The first form can be generically represented as:

$$\begin{aligned}
 & \min [\lambda(x, y)] \\
 & \text{subject to} \\
 & C(x, y) < C^* \\
 & \lambda = \lambda_0
 \end{aligned} \tag{3}$$

where  $\lambda(x, y)$  is a predicted relation of removal of birds ( $x$ ) and of nests ( $y$ ) to population growth,  $C(x, y)$  is a function describing the per-unit costs of  $x, y$ ;  $C^*$  is a cost constraint that cannot be exceeded; and  $\lambda_0$  is an initial (pre-control) value for population growth (currently,  $>1$ ).

Alternatively, the problem can be expressed in terms of a cost or effort objective, which is constrained to meet the biological objectives. That is,

$$\begin{aligned}
 & \min [C(x, y)] \\
 & \text{subject to} \\
 & \lambda(x, y) \leq \lambda^*
 \end{aligned} \tag{4}$$

Somewhat counter-intuitively, this approach may be effective when costs are difficult to quantify but nevertheless it is desirable to keep effort as low as possible. Depending on the situation, we will consider both forms.

### 2.4 Control Model

Our expression of the relationship of the controls to population growth rate requires further elaboration. This relationship is closely related to our seasonal model of population growth, as parameterized by the reverse-time capture–recapture analysis. Recall that  $\lambda$  has 2 components, survival ( $\phi$ ) and recruitment ( $f$ ), and that the relative contribution of these to  $\lambda$  is captured by the parameter  $\gamma$  (throughout this development we assume that  $\phi = S$ , i.e. that permanent emigration is negligible; we relax this assumption later by invoking the results from the joint recapture-resighting analysis). Furthermore,  $\gamma$  can be used to model the proportional change in  $\lambda$  that would occur due to a proportional change in either  $\phi$  or  $f$  (Williams et al. 2002). In our case, we have these relationships estimated over 2 separate, approximately 6-month periods of the year, one (winter–summer) in which reproduction is important, and the other (summer–winter) in which it is negligible. If we define  $\lambda$  over a single 6-month period, the relationship between our controls  $x$  and  $y$  (which are proportional decreases in  $\phi$  and  $f$ , respectively), is

$$\lambda(x, y) = \lambda_0 [1 - x\gamma - y(1 - \gamma)]$$

where

$$x = \frac{\Delta\phi}{\phi_0}, y = \frac{\Delta f}{f_0} \tag{5}$$

and  $\phi_0, f_0$  are the current values and proposed reductions, respectively in  $\phi$  and  $f$ .

In our model, demographic parameters are specific to each 6-month period, which in turn has relevance for decision making. We allow “recruitment” to occur during both periods, but assume that it is principally due to reproduction during the first period (and thus subject to control via nest removal) but due to immigration during the second period (and thus not subject to control via removal). Over the first (winter–summer) period when recruitment is significant we have

$$\lambda_1(x_1, y) = \lambda_{01} [1 - x_1\gamma - y(1 - \gamma_1)].$$

whereas over the second (summer–winter) period, when reproduction is negligible, we have

$$\lambda_2(x_2) = \lambda_{02} [1 - x_2\gamma_2]$$

Finally, annual population growth is obtained as the product:

$$\begin{aligned} \lambda_1(x_1, y) \times \lambda_2(x_2) &= \lambda_{01} [1 - x_1\gamma_1 - y(1 - \gamma_1)] \lambda_{02} [1 - x_2\gamma_2] \\ &= \lambda_0 [1 - x_1\gamma_1 - y(1 - \gamma_1)] [1 - x_2\gamma_2] \end{aligned} \quad (6)$$

where  $\gamma_1$ ,  $\gamma_2$  are the proportional contributions of survival to population growth during the first (winter–summer) and second (summer–winter) periods, respectively.

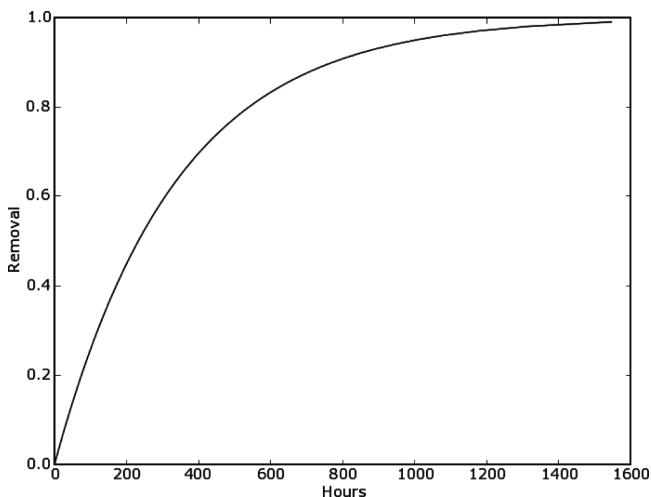
## 2.5 Cost Functions

We could quantify costs for some of our controls, but others were problematic. First, we have estimates of the time and other costs needed to trap a given number of birds, and have related this to our estimates of trapping success. Our records of trapping efforts in 2005 and 2006 indicated that approximately 54.6 h of effort were required to achieve the current capture rate of approximately 0.15; these hourly costs are in addition to fixed costs of trapping (traps, feed, and so forth) and that we need a trap for each main colony. We modelled the relationship of capture (removal) rate to increasing effort via a simple exponential model (Williams et al. 2002: 320) as

$$\Delta\phi = p = 1 - \exp(-kf) \quad (7)$$

where  $p$  is capture rate,  $f$  is effort (in this case, hours), and  $k$  is a coefficient relating effort to success. Equation (7) is easy to solve for  $k$  given specified  $p$  and  $f$ , providing for an estimate of  $k = 0.00297$  given  $p = 0.15$  and  $f = 54.6$ . These relationships can provide an idea of the effort needed to obtain specific reductions (Fig. 3). For instance, 50, 75, 90, and 99% would be predicted to require 232, 465, 773, and 1547 h, respectively. More or less time-efficient procedures would of course result in different values for  $k$  and these predictions, but we would expect a similar





**Fig. 3** Capture-effort relationship: hours of removal effort in relation to removal rate for Monk Parakeets in Barcelona, Spain, 2003–2006

relationship of cost to effort over a wide range of abundance and removal efforts. We recognize that equation (7) requires the assumption of a constant relationship ( $k$ ) between a unit of effort ( $f$ ) and capture rates ( $p$ ); however, we have no information on which to base a more realistic model, for instance allowing for a saturation effect of removal. In the Section 4 we describe how this assumption may affect the generality of our results, and offer recommendations for further work.

### 2.6 Optimization Solution

We used a combination of graphical examination, nonlinear optimization, and simulation-optimization to find control strategies that met our objectives. Because we anticipated that control via nest removal, although potentially effective, would be costly and socially unacceptable (Neidermeyer and Hikey 1977; Van Bael and Pruett-Jones 1996), we first sought to explore the proportional reduction in recruitment or survival required to maintain  $\lambda$  at a specific level  $\lambda^*$ , where  $\lambda^*$  is presumed to be a reduction from the initial (pre-reduction) growth rate of  $\lambda_0$ . Under this special case of equation (2), the relationship between  $x$ ,  $y$  and  $\lambda$  is completely specified by equation (6). For this analysis, we made the additional assumption  $x_1 = x_2 = x$ ; that is, proportional reduction in survival is the same during both seasons. With this proviso, the constraint  $\lambda = \lambda^*$  provides the solution

$$y = \left[ 1 - x\gamma_1 - \frac{\lambda^*}{\lambda_0(1 - x\gamma_2)} \right] (1 - \gamma_1)^{-1} \tag{8}$$

for specified values of  $y$ . By plotting  $y$  on  $x$  for selected values of  $\lambda^*$  (e.g., 1.00, 0.95, and 0.90), we can visually determine combinations of  $x$  and  $y$  that achieve the objective, and, for instance, rule out those that are clearly impracticable.

The above is a useful first step in our decision analysis, but does not consider the relative costs of means of reducing population growth. As suggested above, and according to previous experience in the U.S.A., removal of nests – the principal means of reducing  $f$  – may be an unpopular means of reducing growth rates, causing serious political problems (Temple 1992; Van Bael and Pruett-Jones 1996). Our second decision analysis instead assumes that reduction is by means of removal, principally by trapping, and considers how removal effort should be allocated between seasons. We recast equation (2) so that the decision variables were achieved reductions in survival during each season ( $\Delta\phi_1, \Delta\phi_2$ ), and changed the inequality constraint to an equality constraint. The former is required for application of our effort-removal relationship (equation 7), and the latter greatly simplifies the search for optimal solutions. The recast decision problem is

$$\begin{aligned} & \min [C(\Delta\phi_1, \phi_2)] \\ & \text{subject to} \\ & \lambda(\Delta\phi_1, \Delta\phi_2, \Delta f_0; f_0, \phi_0) = \lambda^* \end{aligned} \quad (9)$$

where

$$C(\Delta\phi_1, \Delta\phi_2) = \sum_{i=1}^2 [-\log(1 - \Delta\phi_i)/k]$$

and the constraint is satisfied by

$$x_1 = \left[ 1 - y_0(1 - \gamma_1) - \frac{\lambda^*}{\lambda_0(1 - \gamma_2 x_2)} \right] \gamma_1^{-1} \quad (10)$$

where

$$x_i = \frac{\Delta\phi_i}{\phi_{0i}}, y_0 = \frac{\Delta f_0}{f_0}$$

and  $\Delta f_0$  is a specified, constant reduction in recruitment, which for the purposes of exploring allocation of removal effort can be set to zero. This problem could be solved by nonlinear optimization, for example using Lagrangian multipliers (Taha 1976; Williams et al. 2002). However, because there is a single constraint and 2 control variables, it is easy to solve by substituting the constraint for one of the control variables. Thus, we replaced  $x_1$  by equation (10) and from equation (9) obtained the value of  $\Delta\phi_2$  that minimized  $C(\Delta\phi_1, \Delta\phi_2)$  via direct search; this value satisfies the constraint, and therefore is optimal. However, the above presupposes that  $\lambda_0 > \lambda^*$ ; if instead  $\lambda_0 \leq \lambda^*$  then the optimal decision by definition is no action ( $\Delta\phi_1 = \Delta\phi_2 = 0$ ). Although this condition appears to be pathological, it does

arise in the course of stochastic simulations under parameter uncertainty (below). Finally, there are situations where no solution is feasible; that is, no combination of removal actions is sufficient to achieve  $\lambda^*$ . These could occur, for instance, if recruitment alone produces  $\lambda > \lambda^*$ , and again can arise in the course of stochastic simulations.

Although the above approach leads to a rational way to explore candidate decisions about control, it is fundamentally dependent on assumed values for the underlying parameters- namely, seasonal survival ( $\phi$ ), reproduction ( $f$ ), and the derived parameters  $\lambda$  and  $\gamma$ . However, these parameters are not known, but rather are estimated from field data and stochastic models, with varying degrees of statistical reliability. Furthermore, the parameters themselves can and likely do vary over time. Optimization should therefore take into account this stochastic uncertainty, because it potentially will influence decision making. Formal approaches exist in which uncertainty can essentially be added as another constraint to the decision model (Taha 1976); however, these can be extremely complicated to solve. We instead use a simulation-optimization approach, which contains the following steps:

- The objective function and constraints are defined as for the deterministic problem.
- Uncertainty in model parameters is characterized by probability distributions, and a random draw is made of a vector of parameter values.
- An optimal decision and objective value are obtained based on these parameter values.
- The process is repeated a large number (e.g., 10,000) of times and the distributions of the decision variables and objective values examined.

Specifically, we computed standard errors for each parameter  $\theta$  that incorporated statistical and temporal variation, by

$$SE(\theta) = \sqrt{\sum_i [(\hat{\theta}_i - \bar{\theta})^2 + SE(\hat{\theta}_i)^2]} \tag{11}$$

where  $\theta$  is the parameter of interested (seasonal  $\phi$  or  $f$ ),  $\hat{\theta}_i$  is the estimated parameter for the  $i$ th study year,  $SE(\hat{\theta}_i)$  is the estimated sampling variance for  $\hat{\theta}_i$ , and  $\bar{\theta}$  is the average of the estimates over the  $k$  study years ( $k = 2$  or  $3$ , depending on the parameter). These values were used to draw normally distributed random variables  $x_i = g_i(\theta)$ , where  $g_1(\phi) = \log\left[\frac{\phi}{1-\phi}\right]$ ,  $g_2(f) = \log(f)$ , with  $\text{var}(x)$  obtained by delta approximations under the appropriate transformation. The random variates  $x_i$  were then back-transformed via  $g_i^{-1}(\theta_i)$  to obtain random values for  $\theta$  and  $f$ , which in turn were used to calculate  $\lambda$  and  $\gamma$ . This approach provides optimal decision solutions for each selection of random variates, but is not a formal, stochastic optimization, which would require more computationally intensive methods (Williams et al. 2002). We performed all decision model computations using Enthought Numeric Python version 2.4 (<http://python.org>).

### 3 Results

#### 3.1 Survival, Recruitment, and Population Growth

We initially attempted to fit several Pradel models to the full Robust CR data structure, using Huggins heterogeneity estimators in MARK. Because of numerical instability, particularly for capture and abundance estimates within primary periods, we modified our approach to a Pradel symmetry model with survival and recruitment parameters constrained to be closed across secondary periods. This eliminated abundance estimates (which were not of primary interest in this analysis) but retains estimates of  $\phi$  and  $f$ . This model fit as evaluated by program RELEASE; however, our bootstrap simulations revealed mild overdispersion, and we used our estimate of  $\hat{c} = 1.10$  to adjust variances and AIC values (Burnham and Anderson 2002). Based on  $QAICc$ , we selected model  $\phi(t)f(t)p(t)$  (Table 2); the resulting point estimates of  $\phi$  and  $f$  were similar to those from the full Robust analysis, but confidence intervals were narrower (Table 3). However, apparent survival rates seemed to us to be unrealistically low, particularly during the winter–summer periods; we suspect that this was due to high rates of emigration. This was confirmed by the joint recapture-resighting analysis (Tables 4–5), with survival during both periods variable among years, but generally exceeding 0.90; the global model fit these data adequately, with indication of mild extra-binomial variation ( $\hat{c} = 1.12$ ). We used these estimates of  $S$  in conjunction with the Pradel estimates of  $f$  (Table 3) to obtain estimates of

**Table 2** Model selection for reverse-time capture–recapture analysis of Monk Parakeets in Barcelona, Spain, 2003–2006

Model <sup>a</sup>	$\Delta QAICc^b$	QAICc Weight <sup>c</sup>	Number of parameters
$\phi(t)f(t)p(t)$	0.000	0.796	30
$\phi(t)f(s)p(t)$	4.004	0.107	28
$\phi(s)f(t)p(t)$	4.578	0.081	28
$\phi(p)f(s)p(t)$	7.784	0.016	25
$\phi(\cdot)f(\cdot)p(t)$	32.445	0.000	23
$\phi(\cdot)f(\cdot)p(\cdot)$	655.084	0.000	3

<sup>a</sup>Model subscripts:  $t$  denotes variation in parameter over seasons and years;  $p$  over seasons only (constant across years),  $s$  by period (winter–summer vs. summer–winter), and  $\cdot$  denotes no seasonal or annual variation.

<sup>b</sup>Akaike Information Criterion adjusted for quasi-likelihood factor of 1.10 and small-sample correction.

<sup>c</sup>Model weight based on QAIC (Burnham and Anderson 2002).

**Table 3** Model-averaged estimates of apparent survival and recruitment from reverse-time capture–recapture analysis of Monk Parakeets in Barcelona, Spain, 2003–2006

Year	Period	$\hat{\phi}$	SE	$\hat{f}$	SE
2003–2004	Winter–Summer	0.300	0.078	1.413	0.567
	Summer–Winter	0.633	0.083	0.118	0.173
2004–2005	Winter–Summer	0.391	0.070	0.894	0.259
	Summer–Winter	0.958	0.100	0.154	0.201
2005–2006	Winter–Summer	0.222	0.057	0.484	0.140

**Table 4** Model selection for joint recapture-resighting analysis of Monk Parakeets in Barcelona, Spain, 2003–2006

Model <sup>a</sup>	Delta QAICc <sup>b</sup>	QAICc Weights <sup>c</sup>	Number of parameters
$S(t) F(t) F'(t)$	0	0.948	39
$S(.) F(t) F'(t)$	5.825	0.052	36
$S(t) F(.) F'(.)$	17.389	0.000	34
$S(.) F(.) F'(.)$	18.151	0.000	31

<sup>a</sup>All models have time-specific recapture and resighting probabilities, and recovery probabilities constrained to zero.

<sup>b</sup>Akaike Information Criterion adjusted for quasi-likelihood factor of 1.12 and small-sample correction.

<sup>c</sup>Model weight based on QAIC (Burnham and Anderson 2002).

**Table 5** Model-averaged estimates of survival ( $S$ ), fidelity ( $F$ ) and return ( $F'$ ) from joint recapture-resighting analysis of Monk Parakeets in Barcelona, Spain, 2003–2006

Year	Period	$\hat{S}$	SE	$\hat{F}$	SE	$\hat{F}'$	SE
2003–2004	Winter–Summer	0.971	0.044	0.163	0.056	0.124	0.041
	Summer–Winter	0.853	0.039	1.000	0.002	0.000	0.000
2004–2005	Winter–Summer	0.776	0.055	1.000	0.002	0.600	0.328
	Summer–Winter	0.928	0.037	0.069	0.055	0.245	0.087
2005–2006	Winter–Summer	0.994	0.026	0.184	0.038	0.142	0.036

the derived parameters,  $\lambda$  and  $\gamma$  (Table 6). The estimates reveal both seasonal and annual variation in growth rates and components of growth, with, as expected, a generally a higher proportion ( $1 - \gamma$ ) due to recruitment occurring during the winter-summer period, which encompasses the breeding season. Annualized growth rate over 2003–2005 was  $\bar{\lambda}=2.04$ , substantially higher than crude, apparent growth as reflected by population surveys ( $\bar{\lambda}=1.08$ ), possibly due to recruitment from immigration, but also to the fact that surveys are based on the counts of nests, which are routinely removed by the city council when pruning the trees, potentially resulting in underestimates of abundance. We acknowledge that our estimate of annualised growth rate likely overestimates actual population growth rate, and suggest that the true value is likely lower. Nevertheless, we suggest that our estimates of  $\gamma$  and  $\lambda$  reasonably represent the relative contributions of survival and recruitment, and thus proceeded to use the averages of the seasonal estimates, and standard errors incorporating temporal variability and statistical uncertainty, in our decision model (Table 7).

**Table 6** Estimated population growth and components of population growth of Monk Parakeets in Barcelona, Spain, 2003–2006

Year	Period	$\hat{\lambda}$	SE <sup>a</sup>	$\hat{\gamma}$	SE
2003–2004	Winter–Summer	2.383	0.568	0.407	0.097
	Summer–Winter	0.971	0.177	0.879	0.156
2004–2005	Winter–Summer	1.670	0.265	0.465	0.074
	Summer–Winter	1.081	0.204	0.858	0.160
2005–2006	Winter–Summer	1.478	0.142	0.672	0.064
	$\bar{\lambda}^b$	2.04			

<sup>a</sup>Estimated via delta method from separate estimates of  $SE(\phi)$  and  $SE(f)$ .

<sup>b</sup>Square root of product of estimated seasonal growth rates through summer–winter 2004–2005.

**Table 7** Parameter values used in simulations of Monk Parakeets in Barcelona, Spain, 2003–2006

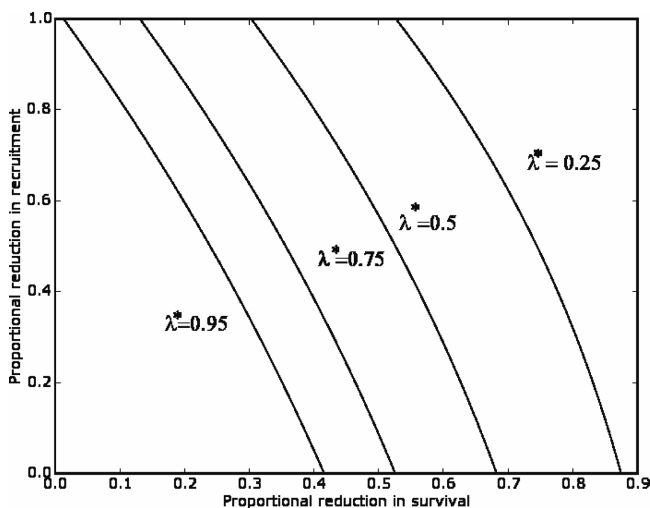
Parameter	Period	$\bar{x}$	SE <sup>a</sup>
$\phi$	Winter–Summer	0.914	0.185
	Summer–Winter	0.891	0.075
$f$	Winter–Summer	0.931	0.917
	Summer–Winter	0.136	0.266
$\lambda^b$	Winter–Summer	1.844	–
	Summer–Winter	1.026	–
$\gamma^b$	Winter–Summer	0.515	–
	Summer–Winter	0.868	–

<sup>a</sup>Incorporates both temporal variability and statistical uncertainty in parameter value.

<sup>b</sup>Estimate based on mean  $\phi$  and  $f$ ; realizations for stochastic simulations use random draws from distributions of  $\phi$  and  $f$ .

### 3.2 Decision Model

Our graphical analysis of combinations of proportional reduction in recruitment and survival resulting in specified values of population growth (Fig. 4) suggests that proportionally less effort is required in lowering  $\phi$  than in lowering  $f$  to achieve the same  $\lambda^*$ . Thus, based on purely biological considerations, the most rapid decrease in population growth could theoretically be achieved by concentrating on decreasing survival rates. Further, nest removal, the main technique for lowering  $f$  may be difficult because of the high synchronicity in breeding phenology of the species and the need to apply control within the last two weeks of the breeding period, to optimize the effort and to reduce time left to the Parakeets for re-breeding. It may also be socially unacceptable in urban areas, in particular because of perceptions



**Fig. 4** Combinations of proportional reduction in recruitment and survival resulting in specified values of population growth ( $\lambda^*$ ) for Monk Parakeets in Barcelona, Spain, 2003–2006, using mean initial recruitment and survival estimates from Table 7

**Table 8** Optimal allocation of removal to seasonal periods for Monk Parakeets in Barcelona, Spain, 2003–2006

$\lambda^*$	Removal allocation <sup>a</sup>		Effort (hours)	Years to achieve 90% reduction
	$p_1$	$p_2$		
0.95	0.0019	0.510	240	44.9
0.75	0.004	0.618	324	8.0
0.50	0.003	0.754	472	3.3
0.25	0.012	0.889	742	1.7

<sup>a</sup> $p_i = \Delta\phi$ ,  $i=1$  (winter–summer),  $2$ (summer–winter)

about abandonment and mortality of pulli during nest removal. By contrast, removal of adults can be accomplished in urban areas by trapping and translocation or euthanasia, and can be done in a way that it less disturbing to the public. We thus shifted focus from allocation of effort between  $\Delta f$  vs.  $\Delta\phi$ , to allocation of removal effort to winter–summer ( $\Delta\phi_1$ ), during which reproduction occurs, and summer–winter ( $\Delta\phi_2$ ), during which reproduction is minimal. We used the constrained optimization approach described earlier to find values of  $\Delta\phi_1$ ,  $\Delta\phi_2$  that achieve  $\lambda^* = 0.25, 0.5, 0.75$ , and  $0.95$ , while minimizing cost. The results indicate that the optimal allocation of removal effort is to allocate the bulk of removal to the summer–winter (Table 8). Costs depend on the desired  $\lambda^*$ , with costs obviously increasing as  $\lambda^*$  decreases, and with the assumed value of  $k$ , with the costs increasing at lower  $k$  (requiring proportionally more removal effort to achieve the same  $\Delta\phi$ ). Assuming that the specified levels of  $\lambda^*$  can be maintained (e.g., there are no density feedbacks), parakeets could be nearly eliminated (reduced by 90%) within <10 years if  $\lambda^* < 0.75$  (Table 8).

The general pattern of these results is confirmed by the stochastic simulations, with median objective values clearly indicating that removal effort allocated to the summer–winter period is optimal (Table 9). Under stochastic assumptions, however, a substantial number of cases arise in which no solution is feasible; i.e., given the parameter values randomly drawn, it is not possible to achieve  $\lambda^*$  via removal. These cases occur, not surprisingly, more frequently as the objective becomes more aggressive, so that at  $\lambda^* = 0.25$ , >25% of simulations had no feasible solution. In a smaller number of cases, simulations resulted in “no action” scenarios; i.e., given the parameter values randomly selected,  $\lambda^*$  had already been achieved without removal; these occurred most frequently under less aggressive reduction objectives (e.g.,  $\lambda^* = 0.95$ ).

### 4 Discussion

In the early 1970’s, the United States Fish and Wildlife Service (USFWS) reduced USA Monk Parakeet population size by half in three years, by an extensive program of removal of nests and shooting of adult birds (Neidermeyer and Hikey 1977; Van Bael and Pruett-Jones 1996). However, the relative success of the different control methods was not evaluated, particularly important when dealing with large population sizes, as it is the case with many current Monk Parakeet populations (Butler 2005). Our demographic analyses and optimizations/simulations suggest

**Table 9** Influence of parameter uncertainty on optimal decisions and objective values for Monk Parakeets in Barcelona, Spain, 2003–2006;  $n = 1000$  simulations,  $k = 0.002977^a$

Objective	$n$	$\bar{x}$	Decision variables and objective value				
			SE	5% quantile	Median	95% quantile	
$\lambda^* = 0.95$ Feasible solutions	803	$p_1$	0.158	0.010	0.0002	0.865	
		$p_2$	0.431	0.010	0.000	0.890	
		Effort	361.450	14.281	29.88	1162.190	
$\lambda^* = 0.75$ No action to meet objective No solution feasible Feasible solutions	69						
	128	$p_1$	0.153	0.010	0.0003	0.832	
	822	$p_2$ Effort	0.508 415.13	0.004 14.483	0.000 56.47	0.529 1179.58	
$\lambda^* = 0.5$ No action to meet objective No solution feasible Feasible solutions	27						
	151	$p_1$	0.169	0.010	0.003	0.869	
	825	$p_2$ Effort	0.613 535.2	0.009 16.045	0.000 135.563	0.655 1371.2	
$\lambda^* = 0.25$ No action to meet objective No solution feasible Feasible solutions	9						
	166	$p_1$	0.217	0.012	0.001	0.882	
	732	$p_2$ Effort	0.669 644.8	0.011 15.44	0.00 219.9	0.948 1378.9	
No action to meet objective No solution feasible	2						
	266						

<sup>a</sup> $k =$  capture coefficient for catch-effort model,  $\lambda^* =$  desired annual population growth rate,  $p_i, i = 1, 2$  is removal rate allocated to winter-summer (1) or summer-winter (2) period.



that the most effective method for reducing parakeet population growth would be removal via trapping or shooting during the summer–winter period, when reproductive recruitment is minimal. Besides being less efficient at reduction, nest removal operations may also be difficult to apply for social and political reasons (Temple 1992; Van Bael and Pruett-Jones 1996). Nest removal operations must also be concentrated in a short period of time of about two weeks, because of the highly synchronous reproduction of the species in our area (Senar and Carrillo-Ortiz 2005) and the need to avoid re-laying. Thus, for both biological as well as social constraints, removal of individuals rather than nests, with efforts concentrated during the summer–winter period, are proportionally more effective at reducing populations. However, we must be clear that these analyses are fundamentally dependent on critical assumptions, some of which cannot be confirmed with existing data.

First, our estimates of demographic parameters ( $\phi$ ,  $f$  and the derived parameters  $\lambda$  and  $\gamma$ ) are, strictly speaking, applicable only to the population of parakeets subject to capture in vicinity of the Museum. Although we think that these rates are reasonably general, and projections based on them agree with the observed population trajectory, other portions of the population in Barcelona and environs may exhibit higher or lower rates. Our examination of resightings of birds marked with visible tags suggests substantial interconnection between the Museum colony and other colonies in Barcelona (Senar and Carrillo-Ortiz 2005). Our analysis of survival and fidelity based on joint recaptures and resightings confirms that emigration from the Museum population to other colonies is high, and that the Museum population also receives substantial immigration from other colonies. However, there is little evidence of regular exchange with populations beyond Barcelona. Future work could focus on CR of birds at multiple colonies, thus providing both colony-specific demographic rates, as well as potentially estimates of movement via multi-state models (Williams et al. 2002).

Second, recruitment and survival are only partially controllable with nest control and removal, respectively. A portion of  $f$  is, by definition, survival of juveniles to 1 year of age; therefore, removal of flight-capable birds at least partially can contribute to  $\Delta f$ . Also, as earlier noted, a portion of  $f$  is contributed by immigration from outside the local population, and therefore, would not be expected to be influenced by removal of nests, unless control is conducted over the full distribution of the species; for Barcelona birds, this would imply city-wide control.

Third, many of our parameter estimates, particularly seasonal growth rates ( $\lambda$ ) but also  $\gamma$ , were estimated with poor precision. More seriously, our data did not allow us to fully evaluate key assumptions underlying our statistical models, so that estimates may not accurately represent the parameter of interest. Specifically, we are reasonably confident in our estimates of demographic survival ( $S$ ) based on the combined recapture-resighting data. However, we suspect that we have overestimated recruitment ( $f$ ), in part because of our inability to disentangle in-situ reproduction from immigration; this may have also led to unrealistically high estimates of seasonal population growth rate ( $\lambda$ ), and potentially could have biased our estimates of  $\gamma$ . This, in turn, would have caused us not only to overestimate the amount of

effort required to achieve specified  $\lambda$  values, but potentially could have misled us in our examination of the relative efficiencies of reductions in recruitment versus survival. The decision model also relies on a very simplistic relationship between effort and trapping success, forced on us by the lack of more informative data on this relationship. If the relationship between removal effort and survival reduction is variable (e.g., a function of density), then our estimates of both absolute and relative cost would be biased. Full exploration of the sensitivity of decisions to these uncertainties would be important to future applications of this approach.

Finally, our models do not incorporate density-dependent feedback or other compensatory mechanisms, and the absence of these components may affect the generality of our conclusions. If, for instance, there is a compensatory response to removal, via density-dependent decreases in other mortality sources, we would expect to see no response of the population to  $\Delta\phi$ , up to a critical value that is determined by a survival in the absence of removal (Anderson and Burnham 1976). Likewise, depression of breeding populations to low levels could trigger a density-dependent increase in recruitment rates, again at least partially nullifying the effects of management. Managers wishing to apply these models to control decisions might be prudent to explore optimal decisions under alternative assumptions, and, if possible, reduce this type of structural uncertainty via adaptive management (Williams et al. 2002).

Our analyses assume that control could be accomplished over a relatively short time span, by means of a sufficiently aggressive removal program. In the absence of such programs the population is predicted to increase rapidly, and our cost equations do not account for the increased difficulties associated with larger densities of parakeets. If “waiting for the future” to control parakeets is a decision alternative, then managers should examine what these future costs might be. Finally, parakeet populations clearly have an intrinsically great capacity for population growth (Muñoz and Real 2006), and it seems likely that populations, if not eliminated, could rapidly expand following cessation of control. Full consideration of the problem thus may require a more formal, dynamic analysis that takes into account uncertainty in dynamics, financial discounting, and other factors in allocating control decisions through time (Taha 1976; Williams et al. 2002).

#### ***4.1 Social Considerations***

The Monk Parakeet is attractive to many people, so that many efforts to control the species have become so contentious that they have been abandoned (Temple 1992; Hyman and Pruett-Jones 1995). In a survey based on 1,800 people in Barcelona city, 80% of people were opposed to the control of the species (Senar and Domènech 2001). However, given the rate of increase and spread of the species in newly established populations (Muñoz and Real 2006), the potential damage that this can cause (Bucher and Bedano 1976; Bucher and Martin 1983; Bucher 1984; Temple 1992; Bucher 1992; Senar and Domènech 2001), and the general consideration of the Monk Parakeet as an exotic invasive species, social considerations should not

prevent the different relevant governmental organizations from controlling of the species. Nevertheless, social considerations complicate the control problem. For this reason, the use of traps, which are more discrete than shooting, may be more advisable in urban environments. Additionally, shooting in urban areas is not allowed by law and may be highly dangerous and contentious.

In rural environments, however, removal by shooting may be a practicable means of reducing  $\phi$ , and may be socially accepted, especially by the farmers who suffer most of the loss. For instance, in 2000–2001, within the agricultural municipality of Gavà, 76 Monk Parakeets were shot in 24 days, because of attacks on maize fields (Departament de Medi Ambient pers. comm.). The costs of removal by shooting will obviously be different from those of trapping. We have no estimates on these costs for parakeet shooting, but note that costs would only affect  $k$  in equation (5), and would not affect either the relative effect of shooting vs. nest removal, or the optimal allocation of shooting between seasons (which should be identical to the optimal allocation of trapping). Since absolute costs would be affected, however, it would be important to quantify these, and ensure that the costs incurred in any removal program were justified by the economic damages avoided. We have mainly focused on the relative costs and benefits of various means of control, on assumption that such control would be economically warranted, because of difficulties in quantifying economic losses from parakeet damage. Future analyses should obtain these cost estimates, and better quantify the total costs of proposed control measures, thus allowing fuller consideration of the economic and social benefits of control.

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